

Ornis Norvegica (2017), **40**: 49–54
doi: 10.15845/on.v40i0.1379

NORWEGIAN ORNITHOLOGICAL SOCIETY

Interspecific aggression by wintering Great Northern Divers *Gavia immer*

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Abstract. Behavioural studies of Great Northern Divers *Gavia immer* wintering on the coast of Jæren, SW Norway in 1996–2010, revealed interspecific aggression by divers against several species of waterbirds. Aggression was shown against two species of cormorants, five species of diving ducks, two species of grebes, one species of diver, one species of alcid, one species of merganser, and against Shelduck *Tadorna tadorna*. In relation to their occurrence in the vicinity of individual Great Northern Divers, piscivorous birds were significantly more often subject to aggression than other waterbirds. Aggression towards piscivorous species was in accordance with predictions from a food competition hypothesis, but possible benefits from threatening and attacking non-piscivorous ducks seem unclear. No support was found for hypotheses related to sexual selection or predation.

Key words: Gaviidae; food competition; seabird winter ecology; piscivory

INTRODUCTION

Great Northern Divers *Gavia immer* are reported to show strong aggression towards waterfowl as well as small mammals on the breeding lakes, not infrequently with fatal results for the attacked individuals, especially in case of ducklings (Sperry 1987, Kirkham & Johnson 1988, Evers et al. 2010). The following four hypotheses for this behaviour were discussed by Kirkham & Johnson (1988): (1) predatory behaviour by the divers; (2) reducing food competition; (3) sexual selection behaviour; (4) non-adaptive behaviour. As the divers in their study did not eat their killed victims, attacked species were non-piscivorous and unlikely as food competitors, and interspecific aggression did not appear to be performed in the presence of a prospective mate during pair formation, no support was found for hypotheses 1, 2 or 3 and the authors tended to favour a non-adaptive hypothesis.

While showing interspecific aggressiveness on the breeding grounds, Great Northern Divers are reported typically to be non-aggressive towards other species in winter (Evers et al. 2010), except in cases where they are attacked by kleptoparasitic gulls (Ford & Gieg 1995, Byrkjedal 2011b). However, during observations of social behaviour of Great Northern Divers wintering on the coast of Jæren, SW Norway (Byrkjedal 2011a), I observed divers showing aggressiveness towards a number of waterfowl species. Great Northern Divers are mainly piscivorous, and aggressiveness towards piscivorous species would be predicted from a food competition hypothesis. Divers wintering in this area

seem frequently to occur in pairs for some time after their arrival in autumn and again from late winter/early spring, and interspecific aggression restricted to adult divers occurring pairwise might indicate behaviour related to sexual selection (strengthening of pair bonds, acquiring new mate). Killing and eating the opponent would indicate a predatory function of the attacks. I here describe the aggressive interactions observed and discuss them in relation to the above hypotheses.

MATERIAL AND METHODS

Behaviour of Great Northern Divers was recorded in the years 1996–2010 during scheduled observation bouts along the c. 60 km coast of Jæren (Byrkjedal 2011a). This open coastline, exposed to the North Sea, has shallow waters with a bottom patchily consisting of sand, cobble and rock. The cobbly and rocky areas are covered by a growth of kelp (*Laminaria* spp). The area holds about 9000–13000 wintering waterfowl, including 40–50 Great Northern Divers, dispersed along the coast (Tysse 1981, Byrkjedal & Eldøy 1984, Follestad et al. 2016). The divers arrive in October–November, presumably from breeding grounds in Iceland and/or Greenland, and depart in April–May. Generally, the birds disperse along the coast, but family groups apparently stay together until December, when also these birds turn to a solitary existence (Byrkjedal 2011a). Pairs start to appear again in mid February.

To cover the coastal stretch of Jæren in search of divers usually took about a week, a new sequence of

the coastline examined each day. Although none of the divers were individually marked, efforts were made to cover the study area during each field bout so as to avoid repeatedly taking observational data from the same individuals. When located, Great Northern Divers were observed for 30 minutes to record any social interactions, and when possible, record time-budgets (Byrkjedal 2011a).

Great Northern Divers in feeding activity can cover long underwater hauls of up to a hundred metres, and likewise when swimming on the surface peering under water to look for prey. Thus, a diver can cover a good stretch of water in short time. The approximate activity areas of 38 divers observed for 30 min plotted on maps measured on average 450 x 200 m (ranges 100–1000 x 10–500 m). The coastline of Jæren consists of shallow bays, within which the Great Northern Divers usually are observed. To get a measure of frequency of species in the vicinity of the divers, all waterfowl swimming in the same bay, up to 200 m from activity areas of divers under observation (as visually judged with the help of maps), were identified and counted, and these

counts were used when testing for randomly directed aggression by the divers in relation to piscivorous and non-piscivorous waterfowl species. In order to avoid bias from unequal numbers of waterfowl present at the different cases when aggression was recorded, the numbers of each species counted within the 200 m radius from an aggressive diver were converted to fractions of 1 (1 representing the total number in each of these cases), and the sum of fractions across all aggressive cases used to arrive at expected values for the tests.

Field work was restricted to days with calm, if possible flat, seas. Ruffled sea and big swells made it difficult to follow the divers. Observations were made from the top of sand dunes and other elevated ground. Spotting scopes (20–45X) and binoculars (10x42) were used.

Observations were dictated to a speech recorder. All interactions between Great Northern Divers and other birds were noted during the observation bouts, and type of behaviour displayed by the divers described. Distances of Great Northern Divers to their victims

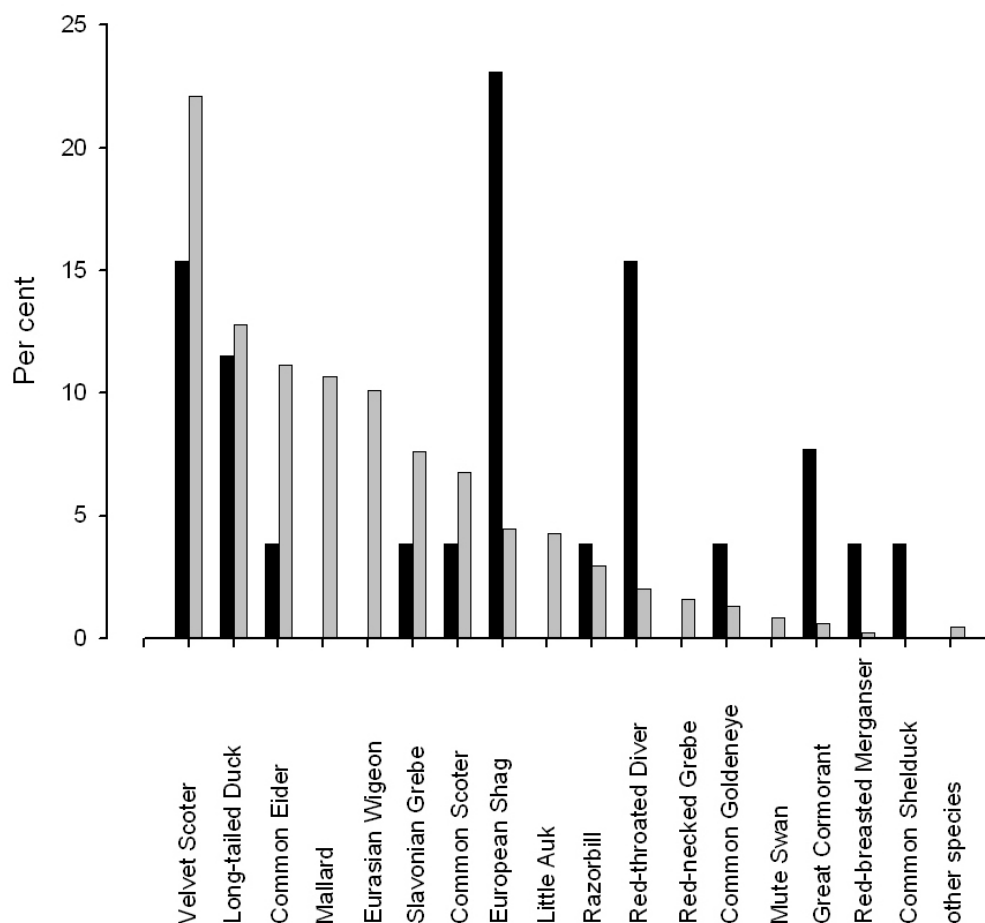


Figure 1. Interspecific aggression towards waterfowl by Great Northern Divers (black columns; $n = 26$) in relation to the relative abundance of waterfowl species in their vicinity (grey columns; n total = 3167). Rarely observed Common Guillemot, Black Guillemot, Surf Scoter *Melanitta perspicillata*, Pintail *Anas acuta*, and Tufted Duck *Aythya fuligula* are lumped in the category “other species”

when aggression started were judged visually, with an attempt to estimate to the nearest metre when distances were less than 10 metres, otherwise to nearest 5 metres. Also the response of victims was recorded. All cases where divers turned and postured towards another bird, upon which the latter gave an evasive reaction, were counted as aggressive behaviour.

RESULTS

Altogether 26 cases were observed of Great Northern Divers showing aggressive behaviour towards 12 other species of waterfowl (Figure 1). The number of swimming waterfowl closer than 200 m from divers performing aggression was on average 122 (± 138 sd, range 11–585). Aggression was performed by divers in October (3 cases), November (15 cases), February (6 cases) and March (2 cases). The date distribution of the 26 cases was not significantly different from the date distribution of field days on which Great Northern

Divers were observed for time budget recordings ($n = 83$ field days; Mann-Whitney $U = 611.0$, $p = 0.415$).

Solitary adults (incl. second winter birds) accounted for 13 cases of aggression (50.0%), juveniles (first winter birds) 10 cases (38.5 %), adults in pairs 2 cases (7.7%), and in 1 case the diver was not aged (3.8%).

None of the attacks involved killing and eating the victim. No case of damage to the victims could be observed.

The divers initiated their aggression on average 23 m (± 19 sd; range 3–50 m) from the opponent, either by (a) approaching with their head held high, bill slanting downwards, (b) neck outstretched in plane with the body, bill directed towards opponent and, (c) underwater attack, bird surfacing at or immediately next to opponent. The postures are shown in Figure 2. In (a) the head position with curved upper part of the neck gives an impression of increased size. Positions (a) and (b) are considered to be threat postures, while (c) represents direct attack. The use of these aggression categories by the divers against waterfowl species is

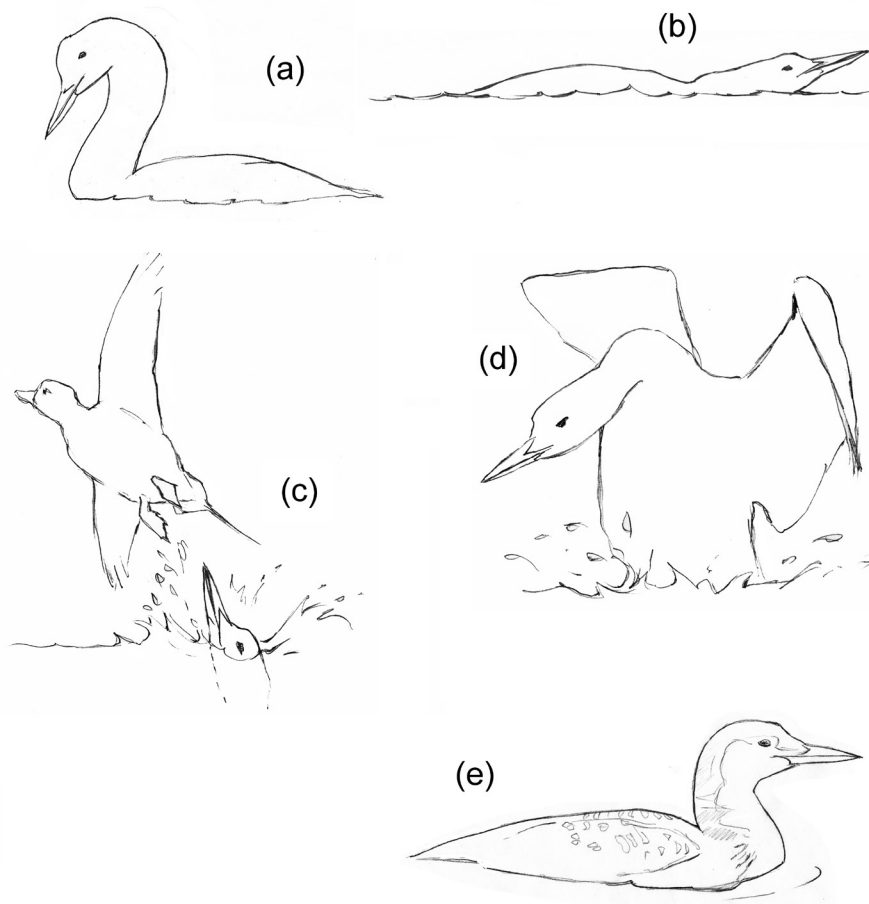


Figure 2. Postures of Great Northern Divers showing aggression toward other species. Threat postures with (a) head held high, bill slanting, and (b) neck in plane with body, bill pointing at victim. Attack (c) from underwater, and post-attack posture (d) similar to “vulturing” (term coined by Rummel & Göttinger (1978) for a type of territorial defence behaviour). For comparison, ordinary swimming posture is indicated in (e). Drawn from field sketches.

Table 1. Number of cases of aggressive behaviour by Great Northern Divers towards other species of waterfowl. Postures (a), (b), and (c) refer to illustrations in Figure 2. Trophic classification from information in Cramp & Simmons (1977).

Waterfowl species	Threat posture (a)	Threat posture (b)	Attack (c)
Piscivorous species			
European Shag	5	1	
Great Cormorant	1	1	
Red-throated Diver	3		1
Razorbill		1	
Red-breasted Merganser			1
Slavonian Grebe			1
Total, piscivorous species	9	3	3
Non-piscivorous species			
Long-tailed Duck		2	1
Velvet Scoter		2	2
Common Scoter		1	
Common Eider		1	
Common Goldeneye			1
Shelduck		1	
Total, non-piscivorous species	0	7	4

shown in Table 1.

Position (a) was observed used against European Shag *Phalacrocorax aristotelis* on five occasions, against Great Cormorant *P. carbo* on one occasion, and against Red-throated Diver *Gavia stellata* on three occasions, each "occasion" representing different individuals of Great Northern Diver. The targeted bird, while immediately watching the posturing diver with alertness, retreated by diving (European Shag, four occasions), swimming away, or taking flight (Red-throated Diver, one occasion). In the latter case the Red-throated Diver surfaced only c. 3 m from a Great Northern Diver which was handling prey at the surface. The Great Northern Diver immediately turned (in position (a)) in the direction of the Red-throated Diver, which assumed a sleek posture, turned away and took flight.

Outstretched threat (b) was observed against Long-tailed Duck *Clangula hyemalis*, Velvet Scoter *Melanitta fusca* (two occasions each), European Shag, Great Cormorant, Razorbill *Alca torda*, Common Eider *Somateria mollissima*, Common Scoter *Melanitta nigra*, and Shelduck *Tadorna tadorna* (one occasion each). The targeted bird responded by quickly swimming away while watching the diver alertly (Long-tailed Duck, Velvet and Common Scoters, Common Eider), diving (European Shag, Razorbill), taking flight (Long-tailed Duck, Great Cormorant), or by showing no reaction (Shelduck). The latter case was counted as aggressive behaviour in spite of the lack of response by the Shelduck, as the posture used by the diver was employed in aggressive interaction against

other species.

Underwater attacks (c) were performed against Velvet Scoter (two occasions), Long-tailed Duck, Red-breasted Merganser *Mergus merganser*, Common Goldeneye *Bucephala clangula*, Slavonian Grebe *Podiceps auritus*, and Red-throated Diver (one occasion each). The response of the victim was to take flight in all these cases, except one case of a Velvet Scoter rushing away from the Great Northern Diver on the surface. In the case of underwater attack on Long-tailed Duck, the diver entered an up-stretched posture with spread wings and lowered neck (posture (d) in Figure 2) as the duck hastily took flight. The Slavonian Grebe attacked from below, was, while flying away, pointed at by the diver in position (b) (Figure 2).

Great Northern Divers turned to aggressive behaviour from preening activity, against Long-tailed Duck (2 cases), Cormorant (1 case) and Red-throated Diver (1 case), and from loafing, against Great Cormorant (1 case). All the other cases of aggressiveness (n = 21) arose from Great Northern Divers that were in food-searching bouts. All the targeted individuals, except of course the Shelduck, were actively diving for food when the divers showed aggressiveness towards them.

The frequencies of species that fell victim to aggressiveness from Great Northern Divers (Figure 1) differed from what should be expected from the waterfowl present within 200 m from the diver, in that aggression was shown significantly more often against piscivorous species (Great Cormorant, European Shag, Red-throated Diver, Slavonian Grebe, Red-breasted

Merganser, Razorbill; 15 of 26 cases) than expected (5 of 26 cases; $\chi^2_1 = 8.124$, $p = 0.004$, two-sided). First winter birds ($n = 10$) showed aggression towards piscivorous species in 70 % of the cases, compared to 44 % in adults, but the difference is not statistically significant (Fisher Exact Test, $p = 0.248$; two-sided).

DISCUSSION

The observations show that Great Northern Divers may attack other species of waterbirds throughout the winter. This behaviour may be more common than previously recognized; one of the threat behaviour (posture (a)) performed by the divers is sufficiently subtle to require a fairly careful observation in order for it to be noticed. While underwater attacks have previously been observed or inferred in interspecific attacks by Great Northern Divers, positions (b) and (d) seems not to have been recorded in aggression against other species before, but these postures are frequently adopted in breeding territory defence against conspecifics and then accompanied by vocalizations (Sjölander & Ågren 1972, Rummel & Goetzinger 1978, Sperry 1987, Kirkham & Johnson 1988). Outside the breeding season Great Northern Divers have previously been observed to attack Red-breasted Mergansers and Herring Gulls swimming by (Tozer 1993). The present paper reports attacks on several species, including Red-breasted Mergansers, but also other ducks.

The bias towards piscivorous birds as victims for aggression indicate that Great Northern Divers attempt to drive away food competitors. None of the aggressive encounters ended in the diver killing their victims. Predation is therefore not a likely cause for interspecific attacks by wintering Great Northern Divers. Aggressiveness was shown by adults as well as juveniles and was distributed throughout the winter, and the aggressive adults were mostly solitary birds. This does not support a sexual selection aspect of the aggression.

While food competition might explain some of the aggression towards other species by Great Northern Divers, the fact that aggression was seen to occur also against diving ducks (Merganser other than Red-breasted Merganser), which hardly can be considered food competitors, seems puzzling. The duck species involved are mostly feeding on molluscs and echinoderms living in soft substrate (Cramp & Simmons 1977, Byrkjedal et al. 2007), irrelevant as prey for Great Northern Divers (Evers et al. 2010). It cannot be excluded, however, that seabirds, piscivorous as well as non-piscivorous, diving near a Great Northern Diver may cause disturbance to potential fish prey, and thus negatively affect the hunting efficiency of the diver. On the other hand, fish startled by diving birds might be even more exposed to detection by the diver, as the sandy bottom

over which most of the cases of aggression took place offers no shelter for fish to hide in, except for sandeels *Ammodytes* spp.), that quickly bury themselves in the sand when frightened (e.g. Henderson 2014), and flatfish laying more or less covered in bottom substrate. Actually, flatfish constitute a substantial portion of the diet of Great Northern Divers in the area where the present observations were made (Byrkjedal 2011b). Any effect of piscivorous and non-piscivorous diving birds on the behaviour and availability of fish that are potential prey for Great Northern Divers, however, remains speculative.

Considering the large size of Great Northern Divers compared to most of the ducks present, attacking ducks might incur little costs to the divers, and the threshold for attacking even non-competitors might be low (Sperry 1987). A case of aggression that clearly seemed maladaptive, was the one against a Shelduck, but the duck did not respond and the action of the diver shortly ended.

The way waterfowl composition in the vicinity of Great Northern Divers was recorded gave only a crude estimate of the targets “available” to a diver. A more precise idea of potential targets for aggression would have been obtained, had the species swimming nearest to a diver been recorded throughout each observation bout. The distance of 200 m around the diver to which the waterfowl were counted could only be visually estimated, albeit with the aid of maps and topographic features present on the maps (spits, skerries, buoys, stakes, etc). However, the relatively short observation distances probably reduced the uncertainties of the estimates. The aggressive cases observed in this study took place on average 156 m from land (SD 102, max 350, min 40) as measured from where they were plotted on maps during the field work.

To conclude, interspecific aggression by Great Northern Divers during winter observed in this study most likely is related to fish capture. The observations of attacks towards non-piscivorous diving bird species may indicate that not only potential competitors for fish prey but also species that might affect the abundance and distribution of potential fish prey in a way that the divers’ foraging is hampered, may be subject to attacks. No evidence for predatory behaviour on waterfowl or behaviour related to sexual selection was found.

Acknowledgments. I am most grateful to Mats O.G. Eriksson and an anonymous reviewer for constructive comments on the manuscript.

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Received 31 March 2017. Accepted 14 December 2017